REDEPOSITION OF POLLEN GRAINS IN LAKE SEDIMENT[1]

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ABSTRACT

Evidence from sediment traps shows that in dimictic Frains Lake pollen grains and the bottom mud in which they are contained are resuspended during spring and autumn mixing, while in Sayles Lake, a nonstratified lake nearby, similar quantities of pollen-bearing sediment are resuspended at irregular intervals throughout the year. In the nonstratified lake resuspended material is poorly mixed in the lake water, while in the dimictic lake, during the seasons of water mixing, resuspended sediment is similar in amount, percentage ash weight, and pollen composition at various levels throughout the water column. Resuspension occurs without sorting or differential movement of individual pollen grains. The pollen content of redeposited sediment serves as a tracer, showing that sediment is moved from the littoral zone to the deeper basin of the lake. In the littoral zone annual stirring may involve the uppermost 6–12 mm of sediment; even in the deeper part of the basin, the uppermost millimeter at least is stirred by this process every year.

Redeposition of sediment and pollen has been reported from experiments with sediment traps in Frains Lake, a thermally stratified lake in Michigan (Davis 1968); circulating water stirs and resuspends sediment during the spring and fall seasons of water mixing. This process is capable of redistributing sediment within the lake basin (Tutin 1955) and thus affecting the final distribution of pollen grains in sediment, so it has obvious importance for the interpretation of fossil pollen.

Seasonal measurement of redeposition has been extended to a shallow, nonstratified lake for comparison with Frains Lake. The constrast in timing demonstrates that absence of thermal stratification is essential for extensive redeposition. To evaluate movement of the sediment and its effect on pollen distribution, sediment traps were set at various depths in various parts of both lakes. With pollen grains serving as a tracer, these traps demonstrate the movement of sediment from one part of the lake basin to another. They serve further to detect any sorting due to differential movement that may occur within the pollen component of the sediment, a phenomenon that had been suspected from the uneven distribution of different kinds of pollen within lake basins (Davis et al. 1971). The total amount of pollen deposited in traps at different stations serves to assess the thoroughness of water mixing.

In addition to information on the direction of sediment movement, the amount of movement, and the distribution of pollen within the suspended sediment, the results of the study provide an estimate of the depth to which sediment in lakes is stirred by the action of water currents.

Throughout this paper reference is made to "pollen grains." In fact the reference is to the waxy exine of the grains, which is identifiable taxonomically and which is resistant to decay. Pollen grains filtered from lake water during the flowering season still retain protoplasm, but a few weeks or months later, only the exine remains. Certain exceptional types of pollen are completely destroyed soon after entering the lake by bacteria or fungi (Havinga 1967) or benthic organisms (R. Davis 1969). For example poplar pollen was found in traps during the flowering season, but was virtually absent from the sediment on the lake floor. However, pollen is not destroyed after it has been incorporated in sediment; this is established by the constancy through time of the ratio of pollen grains to silt and clay in the sediment (Davis 1968). It is for

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this reason that pollen serves as a useful tracer for suspension, movement, and redeposition of the sediment as a whole.

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DESCRIPTION OF SITES

Frains Lake (42°20′N, 83°37′W), 12 km northeast of Ann Arbor, Michigan, is about 200 m wide and 500 m long, sloping gradually to a maximum depth of 10 m in the center. There are no inflowing or outflowing streams. The surrounding topography is nearly flat. Quite unprotected from wind, the lake is surrounded by meadows with a relief of only 3–5 m. Ice about 30 cm thick persists for 3–4 months each winter. In summer the water is strongly stratified, with the top of the thermocline at about 4 m. (For more detailed information on topography, *see* Davis et al. 1971.)

Sayles Lake (42°26′N, 84°4′W), near Pinckney, Michigan, and 35 km west of Frains Lake, is similar in area and shape to Frains Lake and, like Frains Lake, has no major inflowing or outflowing streams. However, the lakes do differ in two major ways: 1) Sayles Lake is less than 1 m deep over most of its area and only reaches a maximum depth of 3 m in an area just south of the basin's center, and 2) Sayles Lake is surrounded by woods on three sides with a steep ridge 20 m high along the south shore. Ice cover is similar to Frains Lake, but Sayles Lake never develops thermal stratification.

METHODS

Deposition of lake sediment was measured in traps (Davis 1967, 1968) consisting of 4-liter bottles with mouth openings of 54–90 cm^2, enclosed in cages of wire netting and suspended from a float 2 m above the trap. The traps usually were suspended 2 m above the mud surface; however, in some experiments they were placed in a vertical, ascending series in the water column, held upright by a flotation collar on the uppermost trap. Flotation collars were also used in shallow-water stations.

Sediment traps collect material falling through the water with a high degree of reproducibility. The number of pollen grains collected is directly proportional to the cross-sectional area of the trap opening (Davis 1967); consequently, the amount recovered in the trap can be expressed as quantity falling per square centimeter of cross-sectional area per day during the interval when the trap is exposed.

Net accumulation of sediment over a period of years was measured in short cores (< 1 m long), taken through the mud-water interface with a small piston corer (Rowley and Dahl 1956) or a modified valve sampler (Davis et al. 1971). A characteristic pollen horizon can be identified in the sediment at about 40 cm below the surface. Below this level tree pollen is dominant; above it ragweed pollen comprises 15–40% of the total. The increased clay content of sediments at the horizon suggests strongly that forest clearance around Frains Lake, which accelerated erosion, occurred almost simultaneously with the increase in ragweed pollen. Once this time horizon indicating forest clearance and land settlement has been identified in a core from Frains Lake, sediment above it can be weighed and its contained pollen grains counted, giving a measure of net accumulation per unit area over the last 140 years (Davis 1968; Davis et al. 1971).

REDEPOSITION OF SEDIMENT AND POLLEN

The deep basin of a stratified lake

Sediment traps in the hypolimnion, near the center of Frains Lake, captured from 40,000 to 81,000 pollen grains per square centimeter per year (Davis 1968). This exceeds by a factor of 2–4 the net accumulation measured in sediment cores: Except

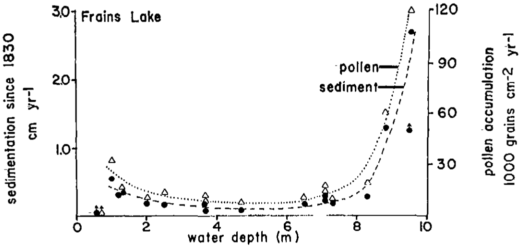

Fig. 1. Average net accumulation rates since settlement in 1830 for pollen (triangles) and sediment (circles) at various depths in Frains Lake.

for a very small deeper area in the center of the lake, sediment in water more than 1 m deep showed rather uniform average yearly rates of pollen accumulation of 8,000 to 21,000 grains per square centimeter (Fig. 1).

The higher rate of deposition in traps than in cores is the result of redeposited sediment. Once deposited into a trap, sediment is retained there and protected from water currents. On the lake floor, however, sediment is often eroded and redeposited; only the net accumulation on the lake floor is measured in cores. The very small deep area in the lake center ($< 2\%$ of the lake area) is protected from erosion by its greater depth. It acts like a trap and measures gross rather than net deposition: Pollen has accumulated there over the last century at an average yearly rate of 64,000–120,000 grains cm^{-2} (Fig. 1), comparable to that in traps.

Traps placed below the thermocline in Frains Lake for 1-month intervals throughout a year showed that deposition of pollen was closely correlated with seasons of water mixing. Pulses of deposition, reaching values as high as 1,000 grains cm^{-2} day^{-1}, occurred during mixing; in contrast, during summer stratification deposition was only 5–6 grains cm^{-2} day^{-1} (Davis 1968). The correlation implies that sediment, resuspended by turbulent water, is an important source of pollen captured in traps.

Two alternative explanations have been tested and rejected. One is that turbulent waters suddenly deposit pollen previously held in suspension. To test this explanation pollen concentration in the lake was monitored at the start and end of the flowering season for ragweed in 1969. On 21 August the surface water contained 1,160 ragweed grains liter^{-1} (range 80–4,654 liter^{-1} in five samples from different parts of the lake); on 24 September the surface water contained only 26 grains liter^{-1} (range 0–56 at the same sampling stations). Clearly pollen concentration in the lake water decreases to low levels well before mixing begins in October; thus the first alternative was rejected.

A second possibility was that out-of-season pollen reaches the lake in large quantities during mixing as dust refloated from the surfaces of vegetation (Tauber 1967). No pollen was present on shrubs surrounding the lake just before the season of heavy pollen deposition during spring overturn, indicating this phenomenon is not important at Frains Lake, which is surrounded by open country and is therefore well exposed to wind (Davis 1968).

The pollen data are corroborated by measurements of total sediment. In two long-term traps (2–3 years) in Frains Lake, the rate of deposition of sediment was 150 and 200 mg dry wt cm^{-2} yr^{-1}, six to eight times the net accumulation of sediment on the lake floor (26 mg cm^{-2} yr^{-1} is average accumulation since settlement at 11 stations). The small deep area in the center of the lake which is protected from erosion again shows deposition rates comparable to those in traps—174–273 mg cm^{-2} yr^{-1}. Sediment there is also very thick (Fig. 1). Not only pollen grains but also enclosing sediments are repeatedly stirred up from the lake bottom and redeposited.

The littoral zone of a stratified lake

Traps were placed in the littoral zone of Frains Lake for short periods to measure redeposition there while the lake was stratified. During August–September 1968, 4–38 out-of-season pollen grains were deposited cm^{-2} day^{-1}; in May, 10–22 out-of-season grains cm^{-2} day^{-1}. These rates are lower by an order of magnitude than redeposition rates in the littoral zone or in

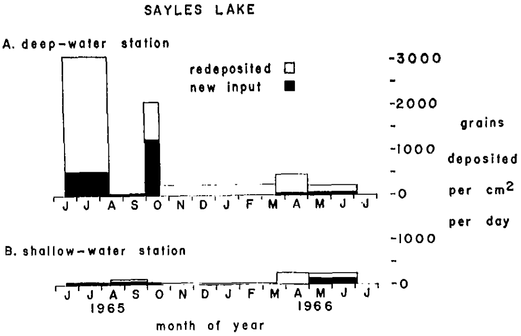

Fig. 2. Pollen deposition in traps in Sayles Lake during the course of the year 1965–1966.

deep water in spring and fall, when the lake water is mixing. The experiments demonstrate that redeposition occurs in the littoral zone while the lake is stratified. Redeposition is small in amount and irregular, however, varying from station to station, indicating incomplete mixing of resuspended pollen in the water. In this respect the results are similar to observations at Sayles Lake (*see below*).

A nonstratified lake

In Sayles Lake, where the water never becomes thermally stratified, traps were sampled at intervals throughout the year 1965–1966 for direct comparison with the samples from Frains Lake. Two stations were used; at the deep (3 m) station the trap was 1.5 m above the bottom, at the shallow (1 m) station it was 0.5 m above the bottom.

Total pollen deposition for the year was 300,000 grains cm^{-2} for the deep-water station and 43,000 grains cm^{-2} for the shallow-water station (Fig. 2). Pollen deposition varied from month to month, with peaks in July–August and September at one station and March–July at the other. The seasonal pulses of deposition in fall and spring, so characteristic at Frains Lake, are missing here. This demonstrates that absence of thermal stratification, permitting mixing of the entire water mass, is essential for extensive redeposition of sediment. At Frains Lake this occurs during seasonal mixing; at Sayles Lake, throughout the ice-free season.

At the shallow station, deposition of pollen during summer was similar in amount to that in the littoral zone of Frains Lake; at the other station, rates were much higher. In general, deposition in the nonstratified lake is highly variable from one month to the next and from one station to another, implying incomplete mixing of the water.

NEW INPUT VS. REDEPOSITION

Pollen in sediment traps is from two sources: redeposited sediment and airborne pollen entering the lake. These two components were separately estimated in traps in the stratified and nonstratified lake throughout the year 1965–1966 to calculate their relative amounts.

Pollen deposited during winter, when no plants are in flower, was used as a standard spectrum of redeposited pollen; this was then used to calculate the absolute amount of redeposited pollen at other seasons. The obviously oversimplified assumption was made that in spring and fall the redeposited pollen is always in the same ratios. Out-of-season pollen was assumed redeposited and substracted from the total in the sample. In-season types of pollen also were subtracted from the total, in the same ratio to the out-of-season types that they occur in the standard spectrum. The remaining pollen was considered new input from the air; at Frains Lake it consisted mainly of ragweed pollen in fall and tree pollen in spring.

During the year of sampling at Frains Lake, 65,000 pollen grains were deposited. Of these, 54,000 (80%) were redeposited, and only 11,000 (20%) were new input to the lake. Confidence in the way these estimates were made is gained from the correspondence of this estimate of new input, 11,000 grains cm^{-2}, to the net increment measured in most sediment cores, 8,000–22,000 grains cm^{-2} (Davis 1968).

I have less confidence in the calculation for Sayles Lake, since the percentages of pollen in redeposited sediment were highly variable, but subtraction from each sample was done using the standard redeposition assemblage derived from deposition during winter months (Fig. 2). In shallow water, the total deposition was 43,000 grains cm^{-2}; of these 13,000 (30%) were estimated as new input, 31,000 (70%) as redeposited. These numbers are similar to those for Frains Lake. At the deep-water station at Sayles Lake, however, 300,000 grains cm^{-2} were collected in the trap during the year. More than half of these were deposited during one 2-month sampling interval—late June through August 1965. Since few major pollen producers flower in midsummer, most of these grains must have been redeposited from sediment. The 117,000 additional grains collected during the rest of the year included 33,000 (30%) new input and 84,000 (70%) redeposited. Over the entire year, about 10% of the total was new input, 90% redeposited.

Conclusion regarding new input and redeposited sediment

The amount of redeposition at Sayles Lake varied greatly from station to station and exceeded that observed in Frains Lake. New input was also variable from station to station, indicating uneven distribution of pollen in the lake water. Circulation patterns and eddies are probably responsible for the uneven distribution of sediment and of new pollen.

The ratio of redeposited pollen to new input, about 4:1 in Frains Lake and 7:3 or 9:1 at Sayles Lake, is isimilar to the ratio between total deposition in traps and net accumulation in cores but is easier to measure over the course of a year. It is therefore a useful and valid indication of the strength of the redeposition process.

SORTING DURING REDEPOSITION

While sediment is suspended in lake water it can be transported laterally from one part of the basin to another. It seemed possible that during transport individual particles, such as pollen grains, might be winnowed from the sediment and transported individually. If this were the case, the pollen grains might be sorted according to their sinking rates, i.e. those with rapid sinking rates would fall close to the source, and those with a slower sinking rate would achieve a longer trajectory. Obviously, this would depend on their size and weight. This process might have explained the variations in pollen in surface sediment from Frains Lake where shallow-water sediment contains high percentages of ragweed pollen and deep-water sediment contains high percentages of oak (Davis et al. 1971). To test this possibility, samplings were made during early spring at various levels in the water column at several stations within the lake.

Table 1. Pollen in Frains Lake water, 30 March 1966

Depth (m)	Native pollen liter^{-1}*	Est. No. Eucalyptus grains added to 16-liter sample before preparation	Eucalyptus grains recovered*
0	177±61	23,300	26,200
5	310±110	23,300	23,800
8	318±83	23,300	28,000

*Estimated from aliquot counts.

Pollen concentration in water in spring

On 30 March 1966, three water samples (16 liters each) were collected from various depths near the center of Frains Lake and filtered through glass filters, which were then prepared by the standard procedures used for sediment (Faegri and Iverson 1964). Pollen was counted and confidence intervals were calculated by the method outlined by Davis (1965). Pollen occurred in low concentrations (200–300 grains liter^{-1}) at all depths in the water column without significant differences between levels (Table 1). Many different types were seen, including ragweed, which were not in flower at that time of year.

Concentrations in the water were lower than expected on the basis of pollen deposition in traps during the same periods. The deposition rate recorded by sediment traps exposed in March and April 1966 was about 200 grains cm^{-2} day^{-1}. To attain this rate with the pollen concentrations noted, it

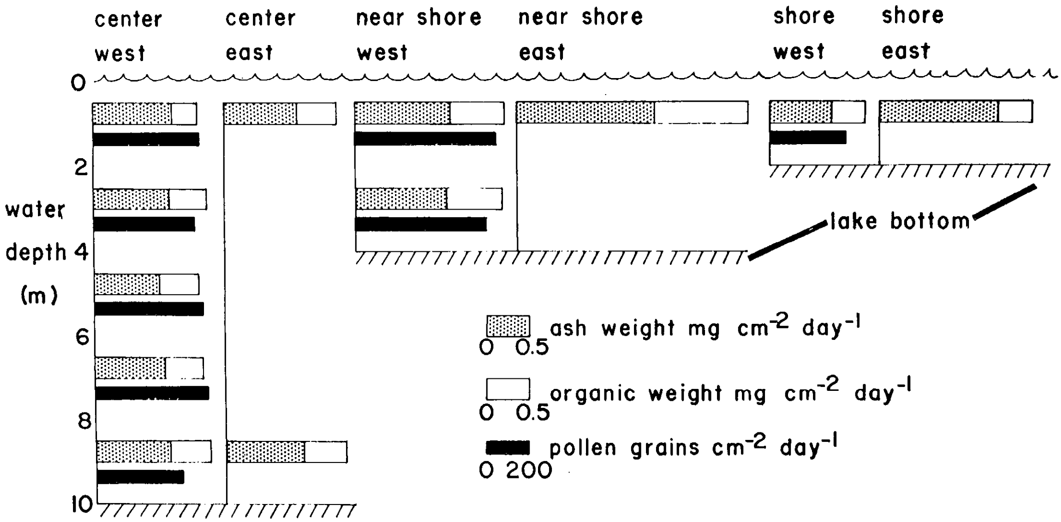

Fig. 3. Sediment and pollen grains captured per square centimeter per day over the interval 25 March–15 April 1968, in 12 traps, at six stations. The depth of the trap below the water surface is shown on the ordinate. Water depth is indicated for each pair of stations.

would be necessary for all the pollen suspended in a column of water 10 m tall and 1 cm^2 in cross section to be deposited each day. Since this is unlikely, I suppose that at intervals the concentrations of pollen in the lake water must have been much higher than those I measured during at least part of the time for which the traps were exposed.

Pollen deposition in water in spring

For a better measure of the distribution of sediment during spring overturn, sediment traps were placed at various depths in the water at several stations in Frains Lake on the first day the ice melted and left there for 3 weeks (25 March–15 April 1968). The water was isothermal at 4°C when the traps were set. Weak stratification developed during the sampling interval. At the end of the experiment, the surface water was 13°C, with an irregular temperature distribution from 2.5 to 7.5 m depth and 9°C in deep water.

Although there was variation between stations, the amount of sediment deposited at different depths at each station was remarkably uniform (Fig. 3). The height of the traps above the sediment surface did not influence the result for ash weight nor for organic weight.

Pollen deposition was measured at three of the stations (Fig. 3). As expected, it was similar at all levels within each station, since most of the pollen was derived from sediment and the amount of sediment was similar at all levels. A component of new pollen from the air is indicated by the presence of poplar (*Populus*) pollen (2.5% of the total pollen in the traps), which was in flower at that time, as were maples. As mentioned above, poplar pollen is not preserved in Frains Lake sediments in amounts higher than 0.5%. The numbers of poplar and maple pollen in the traps were the same at all levels in the water column, as tested by variance analysis of the aliquot counts (variance ratio = 1.96 and 1.88, respectively, df 4,2, $p > 0.05$). This result indicates that the new input of pollen is mixed well in the turbulent water of the lake during overturn. The relative frequencies of all pollen types for both new input and redeposited pollen in the eight traps were homogeneous by the criterion of a chi-square test ($\chi^2 = 88.4$, df 84, $p \simeq 0.25$), implying effective mixing of the water throughout the basin, in contrast to the evidence for incomplete mixing both in the nonstratified lake and in the epilimnion of Frains Lake.

Conclusions regarding sorting

These results disprove the hypothesis of sorting of pollen. The pollen assemblage is resuspended and redeposited as a mixture of all its components, apparently in association with the sediment in which it is contained, without sorting of individual particles. However, these results do not apply to transport of pollen in the water at other seasons before it has become associated with sediment (Davis and Brubaker, unpublished).

Contradictory results have been obtained for Cladocera in an Indiana lake (Mueller 1964). In a similar experiment, Mueller found evidence for cladoceran exoskeletons from the sediment entering a trap 1 m above the lake bottom in preference to traps higher in the water column. It would be useful to repeat these experiments in several different lakes and to compare the behavior of different kinds of sediment constituents.

SOURCE OF REDEPOSITED SEDIMENT

Sediment is stirred up everywhere in the Frains Lake basin, since at all stations (except the deep hole in the very center) deposition into traps is greater than net accumulation in the sediment. It seems intuitively obvious, however, that sediment will be resuspended in greater quantity and at more frequent intervals from the shallowest parts of the lake.

The pollen assemblage in redeposited sediment shows that this is the case. During the spring overturn (25 March–15 April 1968) pollen captured in traps was a mixture of redeposited pollen and new input from the air. These two components were separated to study the pollen percentages within the redeposited component. The subtraction method is the same in principle as described above, except that here new pollen could be estimated from the pollen content of the air. (Pollen had been monitored by Dr. W. Solomon at the University of Michigan hospital in Ann Arbor. I am assuming the pollen in the air near the lake would be roughly similar to that in Ann Arbor over the 3-week interval.) Poplar pollen made up 9.3% of the total

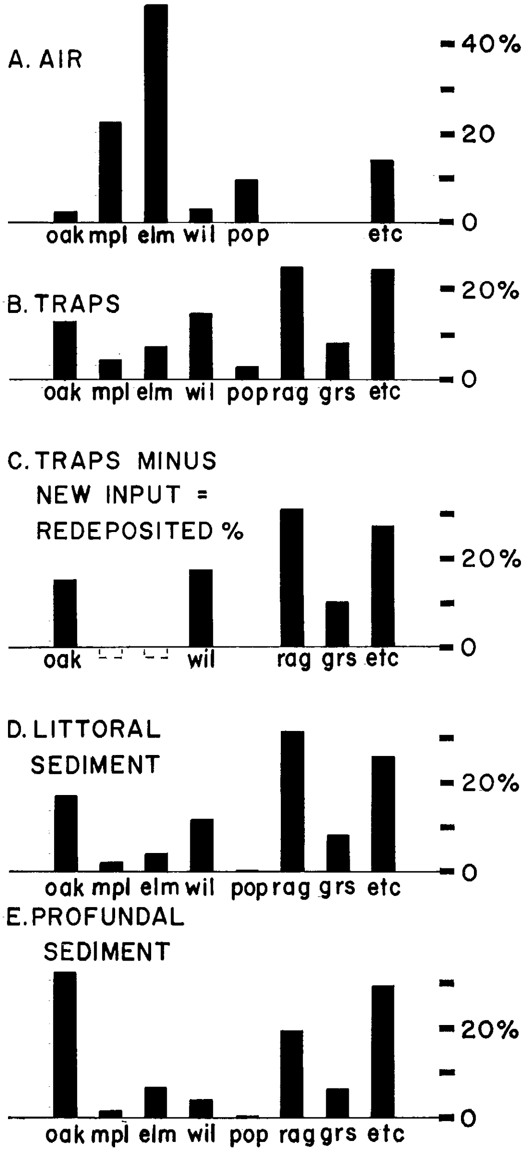

Fig. 4. Frains Lake pollen percentages, 25 March–15 April 1968. A—In the air; B—in trap samples; C—in the trap samples, after subtraction of the new input component. These approximate the pollen percentages in the redeposited sediment captured during this interval. D—In sediment from water depths < 5 m; E—in sediment from water depths > 5 m. Note the similarity between pollen assemblage C and pollen assemblage D.

pollen observed in the air during the period of the experiment (Fig. 4A). Assuming that all the poplar pollen in the sediment traps (Fig. 4B) was new input (since poplar is virtually absent in sediment and therefore in redeposited sediment), I subtracted maple, elm, willow, etc. in the ratios to poplar in which they occurred in the air. (This assumes further that no pollen destruction has yet occurred.) The remaining pollen in the traps was considered redeposited from the sediment. Its percentages were calculated (Fig. 4C) and compared to percentages in surface sediment from various parts of the lake basin—seven samples from the littoral zone and nine from the profundal (Fig. 4D and 4E; Davis et al. 1971). The percentages of redeposited pollen in the traps resemble most closely surface sediment from the littoral zone (Fig. 4D). The relatively high percentages of willow, ragweed, and grass and low oak (10, 30, 10, and 15%) contrast with profundal sediment (4, 20, 6, 32%). The occurrence of trace amounts of *Decodon* pollen (0.5%) in the trap samples may be characteristic, as it is found only in littoral sediment and only in quantity in sediment from the east end of the lake (Davis et al. 1971). I conclude that during April 1968, the prime source of redeposited sediment was the littoral zone. Some or all of the sediment may have come from the east end of the lake.

The pollen assemblage in redeposited sediment can also be identified from the sediment traps exposed throughout winter 1965–1966 in Frains Lake. The percentages varied a little from week to week in November and December before the lake froze, indicating a variety of sources for the sediment, depending probably on wind direction. But in all cases the high percentages of ragweed and willow pollen show that the littoral sediment of the lake, which contains higher proportions of these pollen types than the profundal sediment, is the chief source.

Sediment at Sayles Lake is variable in pollen content, but without a consistent difference between shallow and deeper parts of the lake (Davis et al. 1971), so that the pollen assemblage in redeposited sediment cannot serve as a tracer for sediment source.

DISCUSSION AND CONCLUSIONS

From the results, the following statements can be made:

Redeposition is quantitatively significant, involving stirring to several millimeters' depth

In Frains Lake the ratio of redeposition to new input was 4:1 during a single year of sampling. Deposition into traps in other years was two to four times as great as net accumulation on the sediment surface; i.e. the total amount of resuspended sediment over 1 year was roughly equivalent to 2–4 years' net accumulation. Probably only half this amount (1–2 years' accumulation) is stirred up each year, however, since the sediment stirred up during fall settles before spring resuspension and redeposition begins. On the average, a year's net accumulation is the equivalent of 2–3 mm of sediment (Fig. 1). The uppermost layer has a high water content, so the actual thickness in the first year may be twice this amount. Therefore, the uppermost 6–12 mm may be disturbed each year by resuspension and redeposition in the littoral zone, while the uppermost millimeter, at least, must be stirred up in the deeper parts of the lake.

In Sayles Lake, redeposition was even more extensive, at least at one station. In this shallow lake, both new input and redeposited sediment were variable from station to station. Resuspension may be local in extent and resuspended material incompletely mixed in the lake water. Similar variation was observed in the littoral zone of Frains Lake during summer.

Redeposition is important in the mixing of sediment of different ages

New sediment produced each year is mixed in the water column with older sediment previously deposited. Yearly variation in pollen and sediment inputs to the lake are smoothed out by this process.

Redeposition mixes sediment from different parts of the lake

In lakes in southern Michigan, littoral sediment contains higher percentages of ragweed pollen than does deep-water sediment. Transport of littoral sediment to the center of the lake acts to reduce such differences. In Frains Lake turbulence in the epilimnion in summer effectively prevents primary input of ragweed pollen to deep-water sediment (Davis and Brubaker, unpublished). Redeposited littoral sediment is, therefore, the principal source of the ragweed pollen found in the deep basin of the stratified lake. Similarly, fossil remains of Chydoridae are first deposited in littoral sediment; redeposition carries them out to the profundal regions of the lake (Mueller 1964).

Redeposition moves sediment as a whole, without sorting

Redeposition moves sediment as a whole, including inorganic as well as organic components, although large sand grains and large organic particles may be exceptions. However, I have found no evidence of sorting of individual pollen grains as sediment is lifted from the lake bottom and redeposited.

Redeposition affects net accumulation rates of sediment and pollen

Comparisons of net accumulation rates in several lake basins in southern Michigan indicate that they are variable (by a factor of three in most cases) from one station to another within each lake (Davis et al. 1973), indicating that deposition, resuspension, and redeposition occur nonuniformly within lakes. Frains Lake, for example, shows variation by a factor of 10 (Fig. 1). However, the rates of accumulation of both sediment and pollen are generally higher in deep water than in shallow water. Redeposition involves movement of sediment from shallow to deep water; it reduces accumulation of sediment in the littoral zone and increases accumulation in the deeper regions of the lake. The intensity of resuspension and redeposition in a lake affects the magnitude of this difference. The intensity of redeposition will vary from lake to lake, as the process must be sensitive to lake morphometry and to the strength of local winds, which stir the lake water and cause turbulence at depth during seasons of water circulation.

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